

Reconstructing Disturbances and Their Biogeochemical Consequences over Multiple Timescales

KENDRA K. MCLAUCHLAN, PHILIP E. HIGUERA, DANIEL G. GAVIN, STEVEN S. PERAKIS, MICHELLE C. MACK, HEATHER ALEXANDER, JOHN BATTLES, FRANCO BIONDI, BRIAN BUMA, DANIELE COLOMBAROLI, SARA K. ENDERS, DANIEL R. ENGSTROM, FENG SHENG HU, JENNIFER R. MARLON, JOHN MARSHALL, MATT MCGLONE, JESSE L. MORRIS, LUCAS E. NAVE, BRYAN SHUMAN, ERICA A. H. SMITHWICK, DUNIA H. URREGO, DAVID A. WARDLE, CHRISTOPHER J. WILLIAMS, AND JOSEPH J. WILLIAMS

Ongoing changes in disturbance regimes are predicted to cause acute changes in ecosystem structure and function in the coming decades, but many aspects of these predictions are uncertain. A key challenge is to improve the predictability of postdisturbance biogeochemical trajectories at the ecosystem level. Ecosystem ecologists and paleoecologists have generated complementary data sets about disturbance (type, severity, frequency) and ecosystem response (net primary productivity, nutrient cycling) spanning decadal to millennial timescales. Here, we take the first steps toward a full integration of these data sets by reviewing how disturbances are reconstructed using dendrochronological and sedimentary archives and by summarizing the conceptual frameworks for carbon, nitrogen, and hydrologic responses to disturbances. Key research priorities include further development of paleoecological techniques that reconstruct both disturbances and terrestrial ecosystem dynamics. In addition, mechanistic detail from disturbance experiments, long-term observations, and chronosequences can help increase the understanding of ecosystem resilience.

Keywords: ecosystem ecology, disturbance, fire regime, nitrogen cycling, resilience

Ecological disturbances in terrestrial systems are discrete events that reduce primary producer biomass and strongly regulate material and energy flows. An increasing size or severity of a variety of disturbance types, including beetle outbreaks, storms, and wildfires, has been documented in several studies (e.g., Seidl et al. 2011) during recent decades. This amplification is raising questions about which disturbances are unprecedented and what conditions may lead to threshold behavior in ecosystem responses. It has been particularly difficult to identify incipient shifts in disturbance regimes (Turner 2010). The synergistic effects of interactions among disturbance characteristics, life history parameters, and climate change are of particular concern, because disturbances have potentially important consequences for carbon (C) and nutrient cycling and for hydrology.

We cannot properly evaluate modern disturbance events without the baseline information provided by decadal- to millennial-scale records of disturbances and ecosystem responses. Such long-term records are derived primarily from tree-ring and sedimentary archives, and they allow the reconstruction of past disturbance events and regimes.

When combined with both detailed observational data about individual events and with novel proxies of ecosystem processes, the biogeochemical consequences of changing disturbance regimes can begin to be assessed. An important challenge now is to integrate these two approaches with respect to ecological processes and patterns.

A variety of disturbance agents, such as fire, wind, drought, or insect outbreaks, are familiar to most ecologists as regulating short-term ecosystem processes, such as nutrient cycling and C storage (Pickett and White 1985). These same disturbances can also determine long-term ecosystem trajectories. For example, without soil-replenishing disturbances, productivity may decrease, and ecosystems may retrograde (Wardle et al. 2004). Chronic disturbance, however, can also lead to a long-term reduction of productivity through nutrient depletion (Boerner 1982). Although the importance of disturbances to ecosystem functioning is recognized (box 1), the biogeochemical consequences of disturbances have been particularly difficult to quantify over long timescales. An increasing amount of complementary research now provides the basis for understanding decadal- to millennial-scale ecosystem change, including high-temporal-resolution

Box 1. Background on disturbance ecology.

The theoretical basis for linking biogeochemistry with disturbance ecology was developed in the 1970s and was largely focused on changes from and recovery to steady-state or equilibrium conditions (Vitousek and Reiners 1975). Newer conceptualizations of complex adaptive systems and resilience in ecological systems highlight the important role of interactions, system feedbacks, and landscape contingencies when forecasting how disturbances affect ecosystems. Interactions between biogeochemical cycles and vegetation can reinforce current states or can result in shifts to alternate states, depending on the magnitude and timing of the interactions. Importantly, potential shifts in system states can be caused by the disturbance itself, as well as by centuries to millennia of vegetation–soil feedbacks that constrain, mediate, or amplify ecological responses (Turner et al. 1993).

The concept of *biogeochemical resilience* incorporates the idea that biogeochemical characteristics are spatially differentiated prior to a disturbance, are sensitive to the disturbance event itself, and are coupled to vegetation response patterns and rates (Smithwick 2011). Classically, ecological resilience is focused on organisms, whereas biogeochemical resilience is focused on pool sizes and input or output rates. Over long timescales or across large areas, shifts in biogeochemistry influence vegetation response trajectories and vice versa. Understanding long-term ecosystem resilience to disturbance requires a full characterization of disturbance regimes—the agent or mechanism of disturbance, as well as the magnitude, severity, and return interval (table 1; Peters et al. 2011)—alongside an understanding of elemental pools and flows.

Table 1. Types of disturbances and how they are reconstructed.

Disturbance agent	Severity	Frequency	Reconstruction measure
Fire	Low	High	Fire scars recorded in wood
	High	Low	Tree establishment dates, sedimentary charcoal
Insects	High	Low	Tree demography, insect fossils in sediment
Wind	High	Low	Downed wood, clastic material in sediments
Drought	Variable	Variable	Tree rings, long-term instrumental records, lake level, lake salinity
Tree removal (clearance, deforestation)	High	Low	Pollen preserved in sediment, sedimentation rates, tree demography
Mass movement	Variable	Variable	Sedimentation rate

Note: The key contribution of paleoecology is the reconstruction of enough disturbance events to characterize disturbance regimes. These are often summarized over a given extent and expressed as a distribution or summary statistics (e.g., mean fire return interval). Additional disturbance properties include the spatial extent, the timing, and interactions (Pickett and White 1985).

postdisturbance chronosequences, innovative techniques applied to sediment and tree-ring records to reconstruct past ecosystem change, and long-term ecological measurements of several decades in duration.

The integration of ecosystem processes across multiple timescales is crucial for identifying the biogeochemical consequences of disturbances. Ecosystem ecologists working on the modern landscape (*neocologists*) have had success in quantifying short-term responses to disturbance through direct measurements (Mack et al. 2011). In contrast, paleoecologists have been successful at quantifying past disturbance regimes to contextualize modern disturbances (Marlon et al. 2012). The long-term perspective that paleorecords provide has proven increasingly useful to conservation management (Willis et al. 2007), ecosystem service analyses (Dearing et al. 2012), and restoration ecology. There is now potential to use records of disturbance events and regimes to calculate the biogeochemical consequences of disturbance across climate types, vegetation types, and soil development stages.

Integrating the two views—paleo- and neocosystem ecology—is a challenge because of differences between

disciplines in methodology, timescale, and spatial extent. However, this integration is crucial for understanding the dynamic nature of disturbance and potential feedbacks in the Earth system among climate change, disturbance, and biogeochemistry. Without additional information from paleorecords, extrapolating modern ecosystem responses will likely be ineffective, and direct measurements of ecosystem response are needed in order to interpret the indirect proxies available in paleorecords. Here, we take the first steps toward this integration (a) by reviewing how disturbances are reconstructed, using dendrochronological and sedimentary archives; (b) by summarizing the conceptual frameworks for C, nitrogen (N), and hydrologic responses to disturbances; and (c) by identifying key research priorities for linking the mechanistic knowledge of disturbance from neocology with the long-term perspective granted by paleoecology.

Reconstructing past disturbance

A variety of disturbance events can be reconstructed from annual to millennial timescales (table 1). Disturbance agents

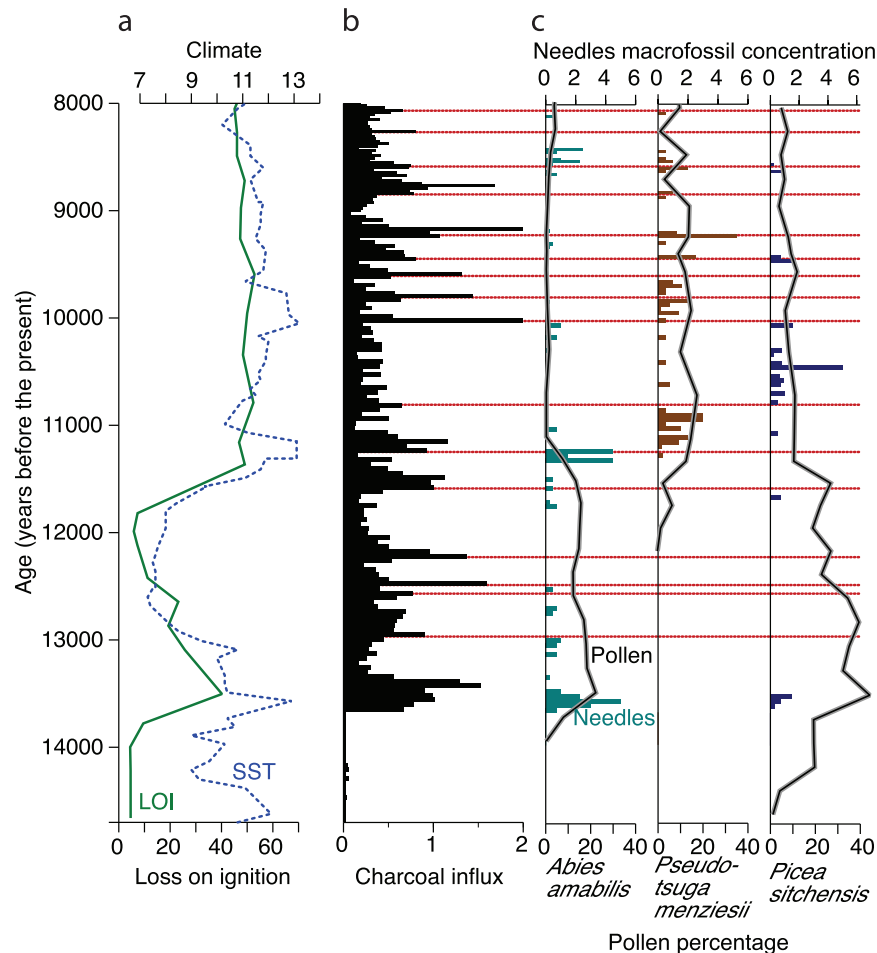


Figure 1. Paleoeological studies capture long-term disturbance histories, state changes in vegetation, and coarse measures of carbon stores. Multiproxy sedimentary data from Yahoo Lake, Washington, show how climate affects biomass and how fire mediates tree species composition during periods of rapid climate change (Gavin et al. 2013). (a) Organic content (loss on ignition [LOI], expressed as a percentage) and climate estimated by sea surface temperature (SST, in degrees Celsius) in the northeast Pacific Ocean. (b) Macroscopic charcoal stratigraphy quantified at 1-centimeter intervals. The red lines indicate inferred fire events near the lake. (c) The percentage of pollen (the black lines) and needle macrofossil concentration (the number of needles per 5 cubic meters of sediment; the colored bars) for three coniferous tree species.

particularly important in midlatitude terrestrial ecosystems are fire, drought, and insect outbreaks. From paleorecords, it is possible to reconstruct the agent, severity, location, and extent of these disturbances. We focus here on records available from tree rings and lacustrine sediment sequences. Long-term instrumental data are helpful for the calibration of potential proxy records. The most robust reconstructions involve either multiple approaches or a detailed calibration data set.

Observational, remote-sensing, and historical records of disturbances offer detailed accounts of a disturbance event's timing, location, and ecosystem impacts, but they typically span only decades or, at most, centuries (Raffa et al. 2008). Tree-ring records can extend this time frame

by providing locally precise, subannually resolved records of low- and high-severity fires (Falk et al. 2011), insect outbreaks (Veblen et al. 1994), and drought (Cook et al. 2004) across a range of forest types. Proxy variables from sedimentary records can provide disturbance reconstructions on even longer timescales, such as over several millennia, but generally have lower resolution.

Fire. Wildfires are the most commonly reconstructed disturbance events from sediment records that span centuries to millennia (Gavin et al. 2007, Higuera et al. 2010). Two aspects of past fire occurrence are focal points for these reconstructions, spanning two spatial scales. Stand-level or local fire occurrence may be interpreted from distinct charcoal peaks in high-resolution sediment records of macroscopic charcoal. For example, fire events in a coniferous montane forest were reconstructed from macroscopic charcoal influx to a small lake basin (figure 1). Several fire regimes can be distinguished over a 6000-year time period. The regional-level amount of burned biomass or area is inferred from standardized summaries of total charcoal accumulation in a record or network of records and quantified as an index (Marlon et al. 2012) or as the area burned (Higuera et al. 2011). The quantity of burned biomass can then be linked to independent proxies for vegetation to infer the fuel types and fire severity.

Fire history investigations based on tree-ring records employ the dating of fire scars, stand establishment, or both, depending on the type of wildfire regime being investigated. Fire-scar networks in western North America have been particularly effective for identifying past landscape and climate drivers of low-intensity fire events (Falk et al. 2011). Mixed-severity fire regimes can be detected with dendrochronological techniques along with reconstructions of fire frequency and the area burned (Hessl 2011).

Drought. Paleorecords can also provide accurate reconstructions of drought conditions. *Drought* is defined in multiple ways on the basis of changes in precipitation, the frequency of precipitation events, and the severity of impacts. Relatively short (less than 200 years) instrumental time series provide data on streamflow, precipitation, soil moisture, Palmer

drought severity index values, flood events, and lake levels (Biondi and Strachan 2012). Dendrohydrology uses growth records from long-lived tree species to extend the contemporary instrumental hydrologic records by one to two orders of magnitude (Stine 1994).

Lake sediment cores further extend the temporal scale of hydrologic reconstruction to millennial and longer time frames. From sedimentary records, droughts can be reconstructed from changes in lake level, diatom communities, and geochemical proxies (Laird et al. 2003). These paleolimnological methods have been most commonly applied to closed-basin lakes in arid or semiarid landscapes in which changes in lake level and salinity are closely related to shifts in hydrologic balance.

Insect outbreaks. During recent decades, irruptive populations of native bark beetles (*Dendroctonus* spp., *Ips* spp.) have exceeded the spatial scale and intensity of past outbreaks by an order of magnitude (Raffa et al. 2008). In western North America, these disturbances have been attributed to the complex interaction of accelerating insect reproductive cycles related to warming air temperatures, decreased tree vigor from moisture deficiencies and concomitant pathogen infestation, and high stand densities of suitable-size host trees (Mitton and Ferrenberg 2012). Tree-ring reconstructions provide evidence that native bark beetles are an essential component of ecosystem function and promote forest regeneration (Sherriff et al. 2011). However, what is believed to be the unprecedented scale and severity of recent outbreaks suggests that neither the dynamics of beetle disturbances nor their biogeochemical impacts are well understood (Rhoades et al. 2013). Longer-term ecological records would help to contextualize the recent episodes. For example, tree-ring records indicate that the recent mountain pine beetle epidemic in central British Columbia was preceded by at least two nineteenth-century outbreaks (Hrinkevich and Lewis 2011). The need to extend the record of past bark beetle disturbances is currently being pursued using lake sediments. Proxy and direct evidence, including pollen and plant and insect macrofossils, has been useful in the reconstruction of past insect disturbances over centurial to millennial timescales (Morris and Brunelle 2012).

Reconstructing biogeochemistry

In addition to aiding in the reconstruction of disturbance regimes, the paleoecological record has the potential to provide key information on ecosystem pools and fluxes. This information is provided through proxy records that range from standard paleoecological techniques to newly developed methods in lacustrine sediment cores (Last and Smol 2001). The pollen record indicates plant community composition, and pollen influx can provide an index of terrestrial biomass. The organic matter content of lake sediment is an indicator of combined lake productivity and detrital terrestrial sources; distinguishing these sources is possible through the C:N ratio. Stable isotopes of C and N also relate to the

cycling and productivity within the aquatic and terrestrial ecosystems. The toolbox of methods is growing rapidly. Newer methods include quantifying the elemental composition of sediments to identify sources of mineral matter, measuring compound-specific isotopes that relate to sources and types of organic matter (e.g., terrestrial, aquatic), and using additional proxies such as magnetic properties to interpret geochemical changes.

Carbon. The cycling of C is a fundamental characteristic of ecosystem functioning, and it is highly sensitive to disturbance. In the absence of change in the disturbance regime, C storage in terrestrial ecosystems is constrained by stable rates of accumulation and degradation. Ecosystems therefore have a characteristic C carrying capacity that may fluctuate at the stand level—that is, the *shifting mosaic steady state* (Bormann FH and Likens 1979). Therefore, over decadal timescales, the net ecosystem C balance (NECB) trends toward zero (Chapin et al. 2006), assuming no directional changes in ecosystem composition or climate. However, changes in the disturbance regime can lead to dramatic shifts in C cycling and NECB. These changes are often realized over long time frames (hundreds to thousands of years) that require a broad and integrated temporal perspective available only from paleorecords or chronosequences. Regional-scale vegetation shifts have the potential to influence the global C balance. For example, 96 teragrams of C accumulated in boreal peatlands during the Holocene (Dean and Gorham 1998). Therefore, one key challenge is to detect and understand how fundamental shifts in disturbance regimes can alter C cycling through ecosystem reorganizations.

Changes in C status may be triggered by unusually severe events, compound disturbances, or major changes in disturbance regimes that exceed the ecological resilience of the system and trigger changes in the vegetation and soil. Therefore, understanding long-term C dynamics in ecosystems requires the integration of contemporary and paleoecological approaches. Studies of the modern landscape are constrained by their narrow temporal context, without baseline information and past histories to fully interpret measured recent changes in NECB. Therefore, it is difficult to determine whether recently observed changes have a precedent or whether they represent novel conditions.

Paleoecological studies capture the long-term patterns in disturbance regimes, state changes in the vegetation, and coarse measures of C stores. The example sedimentary sequence from an old-growth conifer forest shown in figure 1 simultaneously records organic content, changes in fire regimes, and terrestrial vegetation composition—in some cases, in response to rapid climate change. But the nature of proxy records is that they are indirect, and the resolution is often too low to identify precise mechanisms or consequences of change.

For many modern ecosystems, C lost during a disturbance event is largely recovered before the next disturbance, and NECB can be considered relatively stable. The initial driver

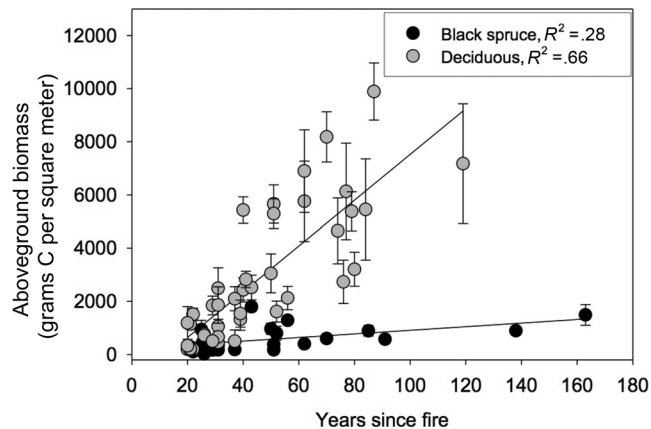


Figure 2. Postfire aboveground carbon (C) accumulation in forests in Alaska. The postfire vegetation type determines the rate of C accumulation in living aboveground biomass. The error bars represent the standard error.

of this trajectory is C fixation in aboveground live biomass, such as wood, with relatively linear rates of C accumulation in the first few decades after a disturbance event (figure 2). However, the subsequent redistribution of this C into soil pools with longer turnover times can take centuries, and these slower processes lead to saturation of the soil pools through C accumulation on those timescales. When comparing data from postdisturbance chronosequences with the paleoecological record, it is clear that both compound disturbances and state changes in the disturbance regime alter these trajectories. In addition, some of these state changes occurred rapidly (e.g., a shift from forest to grassland in less than 300 years; Williams et al. 2010). There are also contemporary examples of incipient shifts in the disturbance regime and model results that predict futures with drastically different C balances (Bond et al. 2005). In short, changes in the disturbance regime can drive state changes in ecosystem structure and function with respect to C storage.

We present a conceptual model of how NECB and disturbance intervals interact over long timescales and how this would be seen in a sedimentary paleorecord (figure 3). Our current understanding suggests that a single disturbance event—even one of high severity, such as a stand-replacing wildfire—will not necessarily alter the long-term C balance. Net primary productivity (NPP) can keep pace with periodic disturbances, and NECB is stable. We recognize that recovery patterns will vary, but we expect that these two processes will usually balance, as is illustrated in figure 3c, in which the time to recover the C lost is plotted with the time since disturbance along a 1:1 line. Slopes greater than 1 imply gains in NECB, and slopes less than 1 imply losses in NECB. Conceptually, we expect ecosystems with a consistent disturbance regime and ecological community to fluctuate around this 1:1 line.

Severe, progressive, or continual deviations away from this 1:1 ratio would indicate a potential biogeochemical

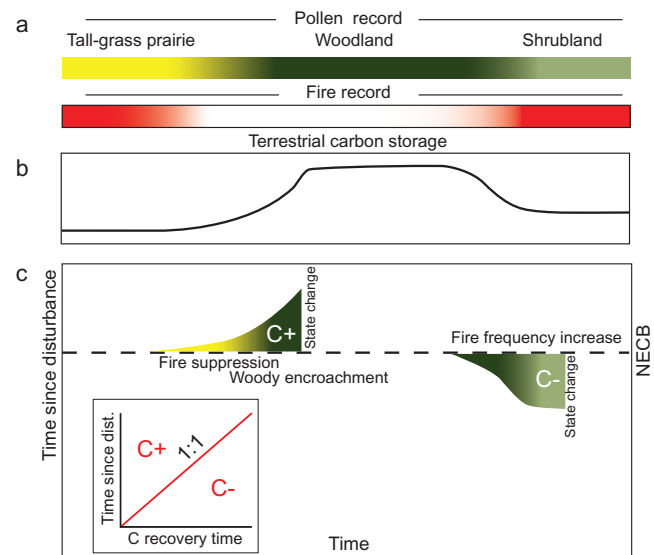


Figure 3. Long-term ecosystem carbon (C) state in the context of disturbance regimes. (a) How this would be recorded in the charcoal and pollen paleorecords of a sediment core. (b) Carbon storage in the ecosystem. (c) The underlying processes of a shift in net ecosystem C balance (NECB), including state changes in vegetation and disturbance regime.

state change (figure 3). We set the 1:1 line as the neutral state at which the C dynamics and disturbance regime are in balance. Perturbations of either the disturbance regime or the time to C recovery would drive the system away from the 1:1 line. When there is a state shift, there is a potential for changes in the C balance relative to the previous system. There is no assumption that the baseline is constant. Indeed, the value of this conceptual figure is to explicitly acknowledge that the baseline changes with a shift in the biogeochemical state. The interpretation of the ratio of the time to disturbance and the time to C recovery is also not interpreted in isolation (Turner et al. 1993); other information from the paleoecological record (e.g., charcoal-inferred change in fire frequency, pollen-inferred change in plant community) is necessary to infer the processes involved.

Small changes in the disturbance return interval can lead to cascading biogeochemical effects, as is demonstrated in the tallgrass prairie ecosystems of North America. This grassland disturbance regime is defined by a cycle of annual fires with the C losses replaced each year (i.e., a 1:1 relationship). If these fires are suppressed by human intervention, the time between disturbances lengthens, leading to net C gain as woody plants increase (a C balance greater than 1). Evidence from experimental burning suggests that lengthening the fire return interval from 1 to 4 years can initiate the first steps of vegetation change (Briggs et al. 2005). The initial C gains are intensified by serial feedbacks that culminate in woody plant encroachment (Knapp et al. 2008).

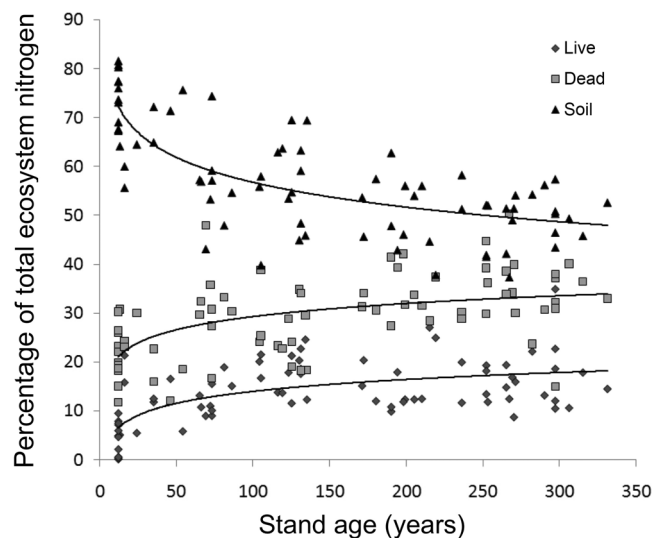


Figure 4. A well-replicated postdisturbance chronosequence of lodgepole pine (*Pinus contorta* var. *latifolia*) forests in the western United States shows an equilibration of ecosystem nitrogen pools but a redistribution of ecosystem nitrogen among the pools after a disturbance. Source: Reprinted with permission from Smithwick and colleagues (2009).

When C ceases to accumulate (the apex of the curve) under the new disturbance regime, we define it as a biogeochemical state change. There is evidence from many other grassland systems that this state change is currently occurring and is leading to increased net aboveground C stocks (Throop and Archer 2008). In these cases, the biogeochemical state change is driven by a shift in plant community composition, which is detectable in the pollen record.

The reverse process has also been seen in the paleorecord. Over time, nonstationary changes in climate (warming and drying) increase the fire frequency and lead to a shorter disturbance interval relative to the C recovery time, which eventually results in a net loss of C and, potentially, to the establishment of a different ecological community. When the C losses stabilize around a new average value, another biogeochemical state change is indicated. Again, this change is driven by a vegetation shift—this time, from woodland to shrubland, such as has been seen in paleorecords from the southwestern United States. It is an open question at this time whether it is possible to get a large change in C balance without a major vegetation shift.

Finally, disturbance and atmospheric carbon dioxide concentrations are tightly linked, with C stored in biomass often released to the atmosphere during a single disturbance event. The rate and mechanism of release varies with the type of disturbance, and, again, NECB may not change in the short term without significant feedbacks to long-term climate change. Human management of fire regimes has been demonstrated to affect C budgets from local to global scales (Bowman et al. 2011).

Nitrogen. Nitrogen dynamics have many similarities with C dynamics after a single disturbance event, and widespread N limitation of NPP and C accumulation often yields close couplings of N and C dynamics after a disturbance (Vitousek and Reiners 1975). However, there are also important differences in the cycling of these two elements that can lead to different long-term trajectories. Nitrogen is more energetically costly to fix than is carbon dioxide, and yet, once it is fixed into an ecosystem, a single atom of N can be recycled to fix many atoms of C. Despite persistent challenges in calculating ecosystem N budgets on decadal timescales, the general paradigm for temperate ecosystems is that, after a single disturbance event, ecosystem N stocks recover to predisturbance levels within decades. Such dynamics have been seen in the postfire chronosequences of *Pinus contorta* forests in the Greater Yellowstone Ecosystem (figure 4; Smithwick et al. 2009). Rapid N accumulation is also demonstrated in the well-studied primary successional chronosequence in Glacier Bay, Alaska, where spruce and hemlock forests accumulated their maximum N contents within 150 years of glacial retreat (Milner et al. 2007). Therefore, on decadal to centennial timescales, a disturbance alone often does not alter long-term nutrient stocks or limitation.

However, the biogeochemical impact of a single disturbance event may also serve to initiate an increase or a decrease in long-term ecosystem N stocks (figure 5a). The disturbance initially causes nutrient loss, but recovery trajectories can vary according to interactions among the disturbance, ecosystem properties, and ecosystem boundary conditions. One scenario is a net long-term loss of N due to disturbance, as in systems in which N fixation is so limited that it cannot replace hydrologic and gaseous N losses. Changes in disturbance intensity or frequency as a result of altered boundary conditions, such as a changing climate or vegetation shifts, may also prevent reaccumulation of N after a disturbance (Yelenik et al. 2013). Alternatively, a disturbance can, in some cases, promote long-term increases in N stocks, such as when robust postfire N fixers like *Alnus* colonize and add more N than is lost in a single disturbance event (Perakis et al. 2011). Similarly, altered boundary conditions, such as a wetter climate, might permit higher N accumulation after a disturbance.

Disturbance-driven increases or losses of nutrients can alter longer-term nutrient limitation when they are considered over long timescales (figure 5b). Each step of this biogeochemical staircase can therefore serve to either increase (*step up*) or decrease (*step down*) nutrient availability. In turn, these disturbance-driven changes in nutrient status fall within a broader biogeochemical template derived from very long-term chronosequences that reveal how ecosystems change over long-term soil development. Whereas soil fertility often increases through primary succession, very old ecosystems ultimately undergo retrogression in the absence of a catastrophic disturbance over millennial timescales (Peltzer et al. 2010). Characteristics of retrogressive ecosystems include reduced availability and amounts of soil nutrients

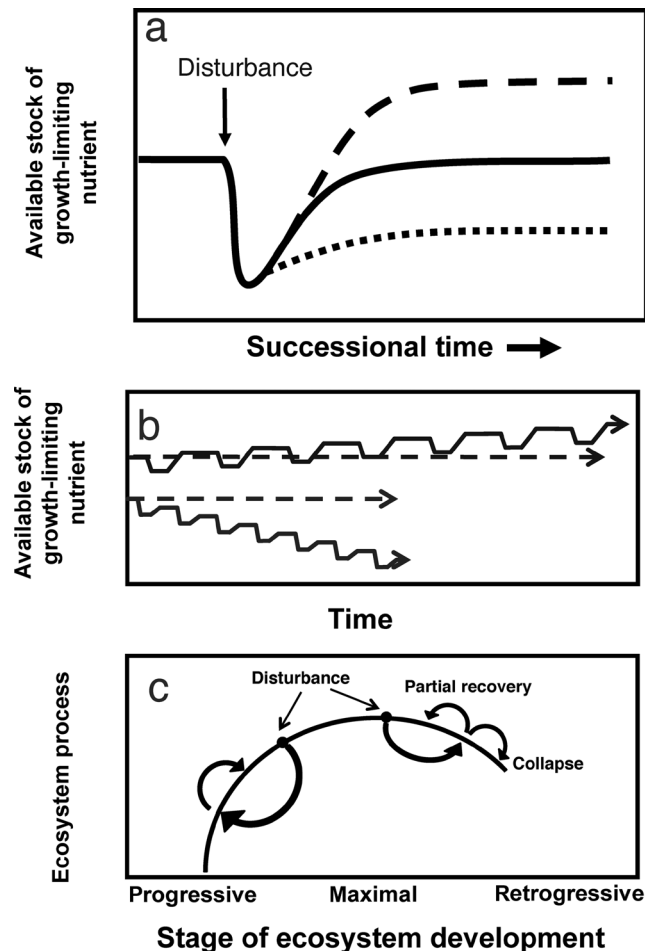


Figure 5. The response of available stocks of growth-limiting nutrients to disturbance. (a) A single disturbance event may serve to increase or decrease or may not affect net stocks of a nutrient, depending on postdisturbance accumulation and loss rates. (b) Over time, a disturbance regime may gradually increase or decrease nutrient availability, a phenomenon that we term the biogeochemical staircase. (c) Over longer timescales, ecosystems often experience the onset of phosphorus limitation and reduced net primary productivity, known as retrogression. In the oldest stages of ecosystems, disturbances can serve to replenish nutrients. Source: Panel (c) was adapted from Peltzer and colleagues (2010).

(notably, phosphorus), reduced NPP, and low standing biomass. In retrogressive ecosystems, disturbance events that expose unweathered soil parent material can replenish available nutrient pools and increase NPP (figure 5c). This seemingly counterintuitive response to disturbance works much the same way as geological uplift, glacial retreat, or volcanism on longer timescales (Porder et al. 2006).

Our understanding of these millennial- and longer-scale processes has been derived primarily from chronosequences, a series of sites with different histories used to reconstruct both primary (soil development) and secondary (stand

development) successional processes. This approach has been very powerful in ecosystem ecology, even if it often provides information only from discrete points in time (Laliberté et al. 2012). Paleorecords—for example, from lake sediment cores—can complement chronosequence studies by providing continuous records that span many millennia (Engstrom et al. 2000). Such records can be used to test theoretical predictions of the conditions under which ecosystems should be responsive to a disturbance and of the direction of the response. Therefore, ecosystems in very early stages of development, in which NPP is limited by N, would be expected to respond differently to a disturbance than would very old, retrogressive ecosystems limited by phosphorus (Peltzer et al. 2010).

There are general patterns in how nutrient limitation shifts from primary succession to very old ecosystems that can aid in the interpretation of paleorecords through time in different landscapes. Nutrient limitation is strong in early stages of soil development and is most commonly driven by N as it slowly accumulates from primary atmospheric sources. Nutrient limitation decreases in the intermediate stages as N accumulates and rock-derived nutrients (e.g., phosphorus, calcium) are released into available forms by weathering. Nutrient limitation intensifies in the late stages of soil development because of the depletion of rock-derived nutrients on geologically old substrates (Chadwick et al. 1999), a shift of the rooting zone from mineral to organic soil horizons (Bormann BT et al. 1995), or the sequestration of accumulated N in unavailable organic forms (Wardle et al. 2012). The sensitivity of ecosystem N cycling and loss to disturbances also changes over geological time. At the young and old ends of the spectrum, N cycling should show weak sensitivity to disturbances, and intermediate-age ecosystems should exhibit strong sensitivity. In early soil development, intense N limitation prevents strong changes in N cycling with disturbances. In intermediate stages of soil development, high rates of biotic N cycling elicit strong responses of N biogeochemistry to disturbances, with a large potential for nutrient losses. Late in soil development, nutrient limitation by rock-derived nutrients (e.g., phosphorus, calcium) intensifies, attenuating the response of N cycling as N limitation is relaxed, which causes a weak response of N cycling and loss to the disturbance. Grounding novel geochemical proxies from sediment records in biogeochemical theory is likely to improve the interpretation of paleorecords in an ecosystem context.

Hydrology. Many studies have documented hydrologic responses to disturbance, and these provide an opportunity to consider ecosystem resilience to a range of disturbance types. A foundational paradigm is that removal of plant biomass, such as in clearcutting experiments, would increase the water available for stream discharge (Bormann FH and Likens 1979). In addition, various ecosystem responses have been observed following disturbances, including changes in water balance (e.g., runoff, recharge, evaporation), chemistry

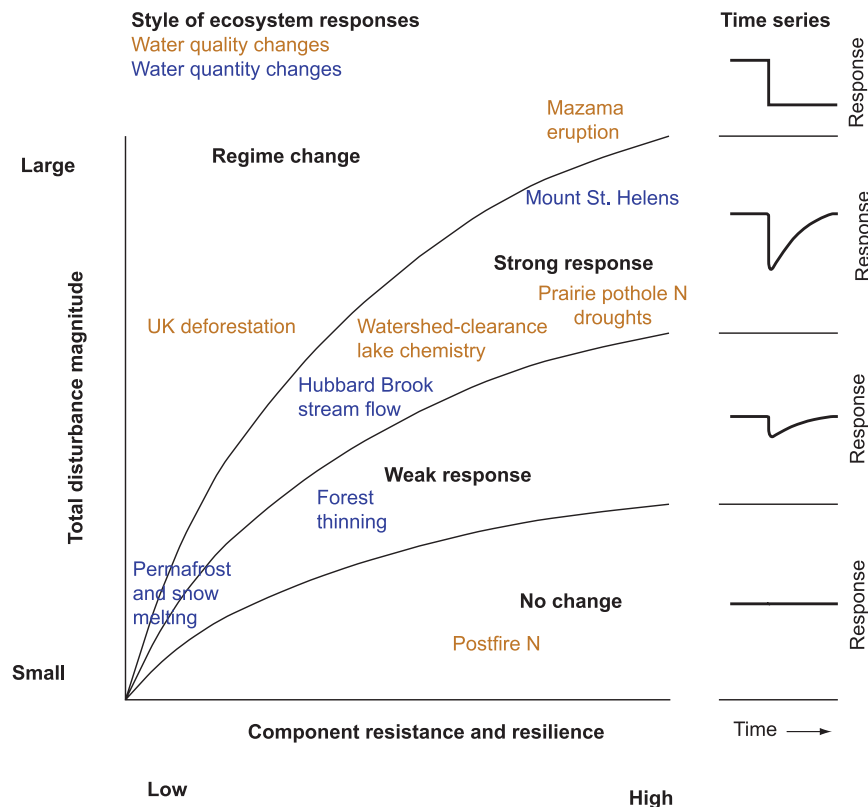


Figure 6. Four types of hydrologic responses to disturbances, encapsulating the range of responses demonstrated in various paleorecords, observations, and modern experiments. Red indicates a response of water quality, and blue indicates a response of water quantity. Abbreviation: N, nitrogen.

(e.g., major ions, nutrients, organic C), and sediment yield. In addition, the responses may vary from regime shifts to no detectable change, depending on the combination of the disturbance magnitude and the resilience of the ecosystem (figure 6). The total disturbance magnitude could represent the effects of a single event but may also indicate the combined consequences of repeated disturbances. The observed examples of responses are highly variable, ranging from regime change to no response.

Land-cover change in different ecosystems reveals the influence of ecosystem resilience and resistance on the scale and style of responses to similar-magnitude disturbances (figure 6). For example, at Hubbard Brook, New Hampshire, the ecosystem resilience of a mesic forest led to an observed recovery of hydrologic behavior in a clearcut watershed within decades (Bormann FH and Likens 1979), but paleoecological studies demonstrate that land clearance can produce persistent change in less resilient ecosystems, such as pine barrens (Lytle 2005), or in combination with other long-term influences, such as climate change, that weaken ecosystem resistance and reduce the range of resilience. However, disturbance severity can also be important for shaping the type of hydrologic response. For example, forest thinning may produce a smaller change than would the total removal of trees.

The importance of small disturbances for producing regime changes and severe responses in systems close to thresholds can be demonstrated by permafrost melt events (Smith et al. 2004) and changes in snowpack-driven stream discharge, in which small amounts of warming can cause the melting threshold to be crossed and can cause a regime change in the system's state and behavior. Consequently, some ecosystems have the potential to jump permanently from one state to another (e.g., when warming is minimal but persistent), even in the face of weak perturbations, whereas others have the capacity to return to their initial state after some period of recovery (e.g., when only a temporary change in watershed functioning occurred).

The frequency of a type of event in a system may predict the magnitude and nature of the hydrologic response. Volcanism provides an example of an infrequent event and of an ecosystem-independent disturbance agent. With no ecosystem feedbacks on disturbance magnitude or frequency, paleoecosystem studies reveal otherwise unknown and infrequent events that cannot be studied over short time frames. For example, the

eruption of Mount St. Helens, Washington, in 1980 had immediate and well-documented effects on the local hydrology, such as the loss of the mountain glaciers (figure 6). Similarly, an ancient eruption in the same region—the eruption of Mount Mazama in 7600 calibrated years before the present—illustrates how volcanism can have far-reaching impacts. The Mazama ash more than doubled the water-holding capacity of soils, which resulted in major vegetation changes, especially in dry sites (Gavin et al. 2001). Posteruption regime shifts in lake level and diatom communities indicate hydrologic changes well to the east, in present-day Montana (Stone and Fritz 2006).

Likewise, paleoecosystem studies reveal that many other historic observations of apparently large or severe disturbances are not unprecedented when they are viewed in a long-term context. Recent drought, fire, and hurricane events have been placed in the context of many past events, which show that large, infrequent disturbances (Foster et al. 1998) are poorly understood without data representing a long time span (Laird et al. 2003). Disturbances that may initially be considered catastrophic, such as the 1988 fires in Yellowstone National Park, may be viewed as natural when they are compared with the paleorecord (Romme et al. 2011), whereas others, such as the 2007 Anaktuvuk River Fire in the Alaskan tundra, may be considered unprecedented over the late Holocene (Hu et al. 2010).

Hydrological responses can also have implications for other biogeochemical cycles in a fashion that depends on the character of the response. For example, severe droughts in the Great Plains have lowered lake levels and limited surface water supply both historically and during the past several millennia (Laird et al. 2003). One consequence of the most severe droughts during the mid-Holocene was to concentrate migrating birds at the few remaining lakes in the Great Plains and to create localized hot spots of nutrient delivery, but because these hydrologic systems are highly resilient, the end of the droughts led to a recovery of the earlier broad distribution of bird stopover locations and nutrient loading (Donovan and Grimm 2007). We suspect that other interactions among systems (e.g., hydrology, fauna, N) and their levels of resilience will produce similarly contingent effects on ecosystem characteristics and function.

However, hydrologic case studies also reveal important absences of responses. This resilience was also seen in long-term ecosystem responses to disturbances of C and N cycling. In particular, several researchers (e.g., Marchand et al. 2009) have sought to document significant changes in water chemistry in lakes following fires in their watersheds and have found little to no change. The absence of such a response has been observed both historically and after repeated fires in the same watershed using paleoecosystem techniques (Marchand et al. 2009). The absence of expected changes illustrates important gaps in our current understanding of ecosystem changes following disturbance.

Research priorities

Here, we identify a number of theoretical and practical approaches to strengthen the insights of ecosystem response to disturbance by linking information across multiple timescales. First, the paleorecord is replete with examples of unexpected complacency to relatively large-magnitude disturbance events (DiMichele et al. 2004). The disturbances can be reconstructed, but a focus on the drivers that allow ecological resilience or persistence is needed (Swetnam and Betancourt 1998). A general framework for identifying ecosystem characteristics that confer resilience has been difficult to achieve. Disturbance experiments may provide a way forward. For example, a large-scale girdling experiment in a secondary temperate forest identified the role of residual vegetation in retaining N and sustaining ecosystem C accumulation over a period during which 20%–50% of the existing trees were experimentally killed (Nave et al. 2011). Manipulations of fire severity can provide insight regarding the magnitude of C loss under different fire regimes and the mechanisms influencing postfire C accumulation in both vegetation and soils. Manipulations of fire frequency can provide insight into the resilience and resistance of different vegetation types to disturbance regimes (Briggs et al. 2005). The results of these types of experiments will add short-term mechanistic detail to long-term pattern-oriented records of past disturbance, providing a powerful joint perspective with which to understand resilience.

Second, it is clear that disturbances of varying magnitudes and types interact at the landscape scale. These interactions have led to the perceived difficulty of predicting multiple successional pathways after a disturbance. Directly studying these interactions can increase our predictive power about postdisturbance biogeochemical trajectories. For example, the interactions of sequential disturbances from logging, fire, and wind in mixed conifer forests in Colorado were nonadditive (Buma and Wessman 2011). Surprisingly, the disturbance agent, combinations, and resilience mechanisms were more important than the number of disturbances. Because multiple disturbance events and agents can be identified in paleorecords, this approach may provide further insight about the interactive nature of disturbance events if they are explicitly studied. A better understanding of how different disturbances are represented in the paleorecord is required. Although fires are well studied and well represented in sedimentary charcoal and tree rings, other important disturbance agents (e.g., insect outbreaks, ice storms, windthrow) are often less clear, despite their having implications for biogeochemical cycles. Identifying the mechanism of disturbance instead of the disturbance type or agent, such as in the conceptual framework described by Peters and colleagues (2011), is likely to improve the predictability of biogeochemical responses.

Several practical avenues can speed the integration of concepts derived from studies of short and long timescales. A central one is to develop techniques to make the sediment record more informative of terrestrial ecosystem dynamics. We identify three main technical developments in paleoecology as high priorities for research: (1) developing improved quantitative proxies of NPP, (2) developing proxies of terrestrial nutrient cycling, and (3) assessing the age and structure of ecosystem C stocks from sedimentary records. There are significant challenges to each of these research areas, but there are also recent advances, such as spatially explicit reconstructions of terrestrial C budgets from pollen records (Boyle et al. 2011), compound-specific N isotopic analysis in sediments (Enders et al. 2008), and rapid high-resolution quantification of sedimentary elemental concentrations (Kylander et al. 2011). Another key is to routinely conduct multiproxy analyses, especially the identification of the source of sedimentary organic matter and the application of whole-lake flux measurements as derived from multiple sediment cores (Engstrom and Rose 2013). Finally, high-resolution temporal sampling across disturbance events, such that disturbances and biogeochemical responses are measured in same record, would be useful.

The primary challenge is to bridge the scales of neoecological and paleoecological studies, to produce a more consistent, synthetic understanding of biogeochemical processes than would be possible from either perspective alone. We identified centurial timescales as the area with the least information on postdisturbance biogeochemical processes but one crucial for the understanding of ecosystem function during the ongoing climate change. Some paleorecords lack

sufficient resolution to capture dynamics associated with several disturbance intervals at a centurial timescale.

The conceptual models developed in this article are largely aspatial but could be made spatial. There are also particular places and spatial scales that may be most synergistic for linking across timescales. For example, the Arctic tundra is a region already experiencing the effects of global change, including altered fire regimes and permafrost melting (Hu et al. 2010). This region is especially promising as a test area for this new synthetic approach to paleoecosystem ecology, because it contains both detailed long-term ecosystem measurements and many sedimentary records of climate, vegetation, and geochemical change.

Conclusions

The unification of long-term ecological monitoring data, chronosequences, and paleorecords provides exciting opportunities for exploring the interactions of multiple disturbance events against a changing background of climate and disturbance frequency. The biogeochemical consequences of a single disturbance are often short lived, with biogeochemical parameters returning to predisturbance conditions on the same timescale as the dominant vegetation type. Therefore, biogeochemical cycles in many ecosystems can be considered resilient to disturbance. The true impact of disturbances may come through changing disturbance regimes, which require the context of long timescales.

Centurial and multicenturial timescales are crucial time frames for improving our understanding of the biogeochemical consequences of disturbances. At this scale is when the understanding of a single disturbance event from a chronosequence begins to break down, whereas the temporal resolution of paleorecords is usually insufficient to capture biogeochemical processes through multiple disturbance events.

Developing proxy records of ecosystem characteristics is a priority for the paleoecological community. Three proxies would be particularly useful: NPP, terrestrial nutrient dynamics, and the age of the ecosystem's C.

The existence of unexpected postdisturbance trajectories, such as multiple successional pathways, continues to challenge ecosystem ecologists and poses a particular problem for the next generation of Earth system models. The empirical and conceptual perspectives described here help move us closer to the goal of increased predictability of postdisturbance trajectories, including incorporating the role of the disturbance agent, severity, and the interactions of those two over centurial to millennial timescales.

Acknowledgments

We thank the National Science Foundation (grant no. DEB-1144879) for funding the PROBE (Paleo Reconstructions of Biogeochemical Environments) workshop, during which these ideas were developed. Any use of trade names is for descriptive purposes only and does not imply endorsement by the US government. We thank Joseph Craine and Fred Swanson for helpful discussion.

References cited

- Biondi F, Strachan S. 2012. Dendrohydrology in 2050: Challenges and opportunities. Pages 355–362 in Grayman WM, Loucks DP, Saito L, eds. *Toward a Sustainable Water Future: Visions for 2050*. American Society of Civil Engineers.
- Boerner REJ. 1982. Fire and nutrient cycling in temperate ecosystems. *BioScience* 32: 187–192.
- Bond WJ, Woodward FI, Midgley GE. 2005. The global distribution of ecosystems in a world without fire. *New Phytologist* 165: 525–537.
- Bormann BT, Spaltenstein H, McClellan MH, Ugolini FC, Cromack K, Nay SM. 1995. Rapid soil development after windthrow disturbance in pristine forests. *Journal of Ecology* 83: 747–757.
- Bormann FH, Likens GE. 1979. *Pattern and Process in a Forested Ecosystem*. Springer.
- Bowman DMJS, et al. 2011. The human dimension of fire regimes on Earth. *Journal of Biogeography* 38: 2223–2236.
- Boyle JF, Gaillard M-J, Kaplan JO, Dearing JA. 2011. Modelling prehistoric land use and carbon budgets: A critical review. *Holocene* 21: 715–722.
- Briggs JM, Knapp AK, Blair JM, Heisler JL, Hoch GA, Lett MS, McCarron JK. 2005. An ecosystem in transition. Causes and consequences of the conversion of mesic grassland to shrubland. *BioScience* 55: 243–254.
- Buma B, Wessman CA. 2011. Disturbance interactions can impact resilience mechanisms of forests. *Ecosphere* 2 (art. 64).
- Chadwick OA, Derry LA, Vitousek PM, Huebert BJ, Hedin LO. 1999. Changing sources of nutrients during four million years of ecosystem development. *Nature* 397: 491–497.
- Chapin FS III, et al. 2006. Reconciling carbon-cycle concepts, terminology, and methods. *Ecosystems* 9: 1041–1050.
- Cook ER, Woodhouse CA, Eakin CM, Meko DM, Stahle DW. 2004. Long-term aridity changes in the western United States. *Science* 306: 1015–1018.
- Dean WE, Gorham E. 1998. Magnitude and significance of carbon burial in lakes, reservoirs, and peatlands. *Geology* 26: 535–538.
- Dearing JA, Yang X, Dong X, Zhang E, Chen X, Langdon PG, Zhang K, Zhang W, Dawson TP. 2012. Extending the timescale and range of ecosystem services through paleoenvironmental analyses, exemplified in the lower Yangtze basin. *Proceedings of the National Academy of Sciences* 109: E1111–E1120.
- DiMichele WA, Behrensmeyer AK, Olszewski TK, Labandeira CC, Pandolfi JM, Wing SL, Bobe R. 2004. Long-term stasis in ecological assemblages: Evidence from the fossil record. *Annual Review of Ecology, Evolution, and Systematics* 35: 285–322.
- Donovan JJ, Grimm EC. 2007. Episodic struvite deposits in a Northern Great Plains flyway lake: Indicators of mid-Holocene drought? *Holocene* 17: 1155–1169.
- Enders SK, Pagani M, Pantoja S, Baron JS, Wolfe AP, Pedentchouk N, Nuñez L. 2008. Compound-specific stable isotopes of organic compounds from lake sediments track recent environmental changes in an alpine ecosystem, Rocky Mountain National Park, Colorado. *Limnology and Oceanography* 53: 1468–1478.
- Engstrom DR, Rose NL. 2013. A whole-basin mass-balance approach to paleolimnology. *Journal of Paleolimnology* 49: 333–347.
- Engstrom DR, Fritz SC, Almendinger JE, Juggins S. 2000. Chemical and biological trends during lake evolution in recently deglaciated terrain. *Nature* 408: 161–166.
- Falk DA, Heyerdahl EK, Brown PM, Farris C, Fulé PZ, McKenzie D, Swetnam TW, Taylor AH, Van Horne ML. 2011. Multi-scale controls of historical forest-fire regimes: New insights from fire-scar networks. *Frontiers in Ecology and the Environment* 9: 446–454.
- Foster DR, Knight DH, Franklin JF. 1998. Landscape patterns and legacies resulting from large, infrequent forest disturbances. *Ecosystems* 1: 497–510.
- Gavin DG, McLachlan JS, Brubaker LB, Young KA. 2001. Postglacial history of subalpine forests, Olympic Peninsula, Washington, USA. *Holocene* 11: 177–188.
- Gavin DG, Hallett DJ, Hu FS, Lertzman KP, Prichard SJ, Brown KJ, Lynch JA, Bartlein P, Peterson DL. 2007. Forest fire and climate change in western

- North America: Insights from sediment charcoal records. *Frontiers in Ecology and the Environment* 5: 499–506.
- Gavin DG, Brubaker LB, Greenwald DN. 2013. Postglacial climate and fire-mediated vegetation change on the western Olympic Peninsula, Washington. *Ecological Monographs* 83: 471–489. doi:10.1890/12-1742.1
- Hessl AE. 2011. Pathways for climate change effects on fire: Models, data, and uncertainties. *Progress in Physical Geography* 35: 393–407.
- Higuera PE, Gavin DG, Bartlein PJ, Hallett DJ. 2010. Peak detection in sediment-charcoal records: Impacts of alternative data analysis methods on fire-history interpretations. *International Journal of Wildland Fire* 19: 996–1014.
- Higuera PE, Whitlock C, Gage JA. 2011. Linking tree-ring and sediment-charcoal records to reconstruct fire occurrence and area burned in subalpine forests of Yellowstone National Park, USA. *Holocene* 21: 327–341.
- Hrinkevich K, Lewis KJ. 2011. Northern range limit mountain pine beetle outbreak dynamics in mixed sub-boreal pine forests of British Columbia. *Ecosphere* 2 (art. 116).
- Hu FS, Higuera PE, Walsh JE, Chapman WL, Duffy PA, Brubaker LB, Chipman ML. 2010. Tundra burning in Alaska: Linkages to climatic change and sea-ice retreat. *Journal of Geophysical Research: Biogeosciences* 115 (art. G04002). doi:10.1029/2009JG001270
- Knapp AK, et al. 2008. Shrub encroachment in North American grasslands: Shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. *Global Change Biology* 14: 615–623.
- Kylander ME, Ampel L, Wohlfarth B, Veres D. 2011. High-resolution X-ray fluorescence core scanning analysis of Les Echets (France) sedimentary sequence: New insights from chemical proxies. *Journal of Quaternary Science* 26: 109–117.
- Laird KR, Cumming BF, Wunsam S, Rusak JA, Oglesby RJ, Fritz SC, Leavitt PR. 2003. Lake sediments record large-scale shifts in moisture regimes across the northern prairies of North America during the past two millennia. *Proceedings of the National Academy of Sciences* 100: 2483–2488.
- Laliberté E, Turner BL, Costes T, Pearse SJ, Wyrwoll K-H, Zemunik G, Lambers H. 2012. Experimental assessment of nutrient limitation along a 2-million-year dune chronosequence in the south-western Australia biodiversity hotspot. *Journal of Ecology* 100: 631–642.
- Last WM, Smol JP, eds. 2001. *Tracking Environmental Change Using Lake Sediments*, vol. 2: Physical and Geochemical Methods. Kluwer.
- Lytle DE. 2005. Palaeoecological evidence of state shifts between forest and barrens on a Michigan sand plain, USA. *Holocene* 15: 821–836.
- Mack MC, Bret-Harte MS, Hollingsworth TN, Jandt RR, Schuur EAG, Shaver GR, Verbyla DL. 2011. Carbon loss from an unprecedented Arctic tundra wildfire. *Nature* 475: 489–492.
- Marchand D, Prairie YT, del Giorgio PA. 2009. Linking forest fires to lake metabolism and carbon dioxide emissions in the boreal region of Northern Québec. *Global Change Biology* 15: 2861–2873.
- Marlon JR, et al. 2012. Long-term perspective on wildfires in the western USA. *Proceedings of the National Academy of Sciences* 109: E535–E543.
- Milner AM, Fastie CL, Chapin FS III, Engstrom DR, Sharman LC. 2007. Interactions and linkages among ecosystems during landscape evolution. *BioScience* 57: 237–247.
- Mitton JB, Ferrenberg SM. 2012. Mountain pine beetle develops an unprecedented summer generation in response to climate warming. *American Naturalist* 179: E163–E171.
- Morris JL, Brunelle A. 2012. Pollen accumulation in lake sediments during historic spruce beetle disturbances in subalpine forests of southern Utah, USA. *Holocene* 22: 961–974.
- Nave LE, et al. 2011. Disturbance and the resilience of coupled carbon and nitrogen cycling in a north temperate forest. *Journal of Geophysical Research: Biogeosciences* 116 (art. G04016). doi:10.1029/2011JG001758
- Peltzer DA, et al. 2010. Understanding ecosystem retrogression. *Ecological Monographs* 80: 509–529.
- Perakis SS, Sinkhorn ER, Compton JE. 2011. $\delta(15)\text{N}$ constraints on long-term nitrogen balances in temperate forests. *Oecologia* 167: 793–807.
- Peters DPC, Lugo AE, Chapin FS III, Pickett STA, Duniway M, Rocha AV, Swanson FJ, Laney C, Jones J. 2011. Cross-system comparisons elucidate disturbance complexities and generalities. *Ecosphere* 2 (art. 81).
- Pickett STA, White PS. 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press.
- Porder S, Clark DA, Vitousek PM. 2006. Persistence of rock-derived nutrients in the wet tropical forests of La Selva, Costa Rica. *Ecology* 87: 594–602.
- Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Turner MG, Romme WH. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. *BioScience* 58: 501–517.
- Rhoades CC, et al. 2013. Biogeochemistry of beetle-killed forests: Explaining a weak nitrate response. *Proceedings of the National Academy of Sciences* 110: 1756–1760. doi:10.1073/pnas.1221029110
- Romme WH, Boyce MS, Gresswell R, Merrill EH, Minshall GW, Whitlock C, Turner MG. 2011. Twenty years after the 1988 Yellowstone fires: Lessons about disturbance and ecosystems. *Ecosystems* 14: 1196–1215.
- Seidl R, Schelhaas M-J, Lexer MJ. 2011. Unraveling the drivers of intensifying forest disturbance regimes in Europe. *Global Change Biology* 17: 2842–2852.
- Sherriff RL, Berg EE, Miller AE. 2011. Climate variability and spruce beetle (*Dendroctonus rufipennis*) outbreaks in south-central and southwest Alaska. *Ecology* 92: 1459–1470.
- Smith LC, MacDonald GM, Velichko AA, Beilman DW, Borisova OK, Frey KE, Kremenetski KV, Sheng Y. 2004. Siberian peatlands a net carbon sink and global methane source since the early Holocene. *Science* 303: 353–356.
- Smithwick EAH. 2011. Pyrogeography and biogeochemical resilience. Pages 143–164 in McKenzie D, Miller C, Falk DA, eds. *Landscape Ecology of Fire*. Ecological Studies, vol. 213. Springer.
- Smithwick EAH, Kashian DM, Ryan MG, Turner MG. 2009. Long-Term nitrogen storage and soil nitrogen availability in post-fire lodgepole pine ecosystems. *Ecosystems* 12: 792–806.
- Stine S. 1994. Extreme and persistent drought in California and Patagonia during Mediaeval time. *Nature* 369: 546–549.
- Stone JR, Fritz SC. 2006. Multidecadal drought and Holocene climate instability in the Rocky Mountains. *Geology* 34: 409–412.
- Swetnam TW, Betancourt JL. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *Journal of Climate* 11: 3128–3147.
- Throop HL, Archer SR. 2008. Shrub (*Prosopis velutina*) encroachment in a semidesert grassland: Spatial-temporal changes in soil organic carbon and nitrogen pools. *Global Change Biology* 14: 2420–2431.
- Turner MG. 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91: 2833–2849.
- Turner MG, Romme WH, Gardner RH, O'Neill RV, Kratz TK. 1993. A revised concept of landscape equilibrium: Disturbance and stability on scaled landscapes. *Landscape Ecology* 8: 213–227.
- Veblen TT, Hadley KS, Nel EM, Kitzberger T, Reid M, Villalba R. 1994. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. *Journal of Ecology* 82: 125–135.
- Vitousek PM, Reiners WA. 1975. Ecosystem succession and nutrient retention: A hypothesis. *BioScience* 25: 376–381.
- Wardle DA, Walker LR, Bardgett RD. 2004. Ecosystem properties and forest decline in contrasting long-term chronosequences. *Science* 305: 509–513.
- Wardle DA, Jonsson M, Bansal S, Bardgett RD, Gundale MJ, Metcalfe DB. 2012. Linking vegetation change, carbon sequestration and biodiversity: Insights from island ecosystems in a long-term natural experiment. *Journal of Ecology* 100: 16–30.
- Williams JW, Shuman B, Bartlein PJ, Diffenbaugh NS, Webb T III. 2010. Rapid, time-transgressive, and variable responses to early Holocene midcontinental drying in North America. *Geology* 38: 135–138.
- Willis KJ, Araújo MB, Bennett KD, Figueroa-Rangel B, Froyd CA, Myers N. 2007. How can knowledge of the past help to conserve the future? Biodiversity conservation and the relevance of long-term ecological studies. *Philosophical Transactions of the Royal Society B* 362: 175–187.
- Yelenik S, Perakis S, Hibbs D. 2013. Regional constraints to biological nitrogen fixation in post-fire forest communities. *Ecology* 94: 739–750.

Kendra K. McLauchlan is affiliated with the Department of Geography at Kansas State University, in Manhattan. Philip E. Higuera and John Marshall are affiliated with the College of Natural Resources at the University of Idaho, in Moscow. Daniel G. Gavin is affiliated with the Department of Geography at the University of Oregon, in Eugene. Steven S. Perakis is affiliated with the US Geological Survey's Forest and Rangeland Ecosystem Science Center, in Corvallis, Oregon. Michelle C. Mack is affiliated with the Department of Biology at the University of Florida, in Gainesville. Heather Alexander is affiliated with the Department of Biological Sciences at the University of Texas at Brownsville. John Battles is affiliated with the Department of Environmental Science, Policy, and Management at the University of California, Berkeley. Franco Biondi is affiliated with the Department of Geography at the University of Nevada, Reno. Brian Buma is affiliated with the Cooperative Institute for Research in Environmental Sciences at the University of Colorado at Boulder. Daniele Colombaroli is affiliated with the Oeschger Centre for Climate Change Research and the Institute of Plant Sciences, at the University of Bern, Switzerland. Sara K. Enders is affiliated with the Department of Land, Air, and Water Resources at the University of California, Davis. Daniel R. Engstrom is affiliated with the Science Museum of Minnesota's St. Croix Watershed Research Station, in Marine on St. Croix. Feng Sheng Hu is affiliated with the Department of Plant Biology at the

University of Illinois at Urbana-Champaign. Jennifer R. Marlon is affiliated with the School of Forestry and Environmental Studies at Yale University, in New Haven, Connecticut. Matt McGlone is affiliated with Landcare Research, in Lincoln, New Zealand. Jesse L. Morris is affiliated with the Department of Geosciences and Geography at the University of Helsinki, in Finland. Lucas E. Nave is affiliated with the Department of Ecology and Evolutionary Biology at the University of Michigan, in Ann Arbor. Bryan Shuman is affiliated with the Department of Geology and Geophysics at the University of Wyoming, in Laramie. Erica A. H. Smithwick is affiliated with the Department of Geography and the Intercollege Graduate Degree Program in Ecology at the Pennsylvania State University, in University Park. Dunia H. Urrego is affiliated with the École Pratique des Hautes Études and with the French National Center for Scientific Research's (CNRS) Oceanic and Continental Environments and Palaeoenvironments joint research unit at the University of Bordeaux, France. David A. Wardle is affiliated with the Department of Forest Ecology and Management at the Swedish University of Agricultural Sciences, in Umeå. Christopher J. Williams is affiliated with the Department of Earth and Environment at Franklin and Marshall College, in Lancaster, Pennsylvania. Joseph J. Williams is affiliated with the Institute of Geography and Earth Sciences at Aberystwyth University, in Aberystwyth, United Kingdom.